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THE OPTIC LOBES OF THE BEE'S BRAIN IN THE LIGHT OF RECENT NEUROLOGICAL METHODS.

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While studying the central mass of the brain of the common honey bee, which I have already described with some detail,[1] there was abundant opportunity offered for noting the finer structure of the so-called optic lobes. From the casual observations then made I take the following notes.

The general form of the optic lobes, as well as the cellular and fibrillar masses composing them, have been fairly well described by Berger, Viallanes and others for other hexapods, and what one finds in the bee does not differ materially from these early descriptions, so far as the inner two fibrillar masses are concerned (f. m. 2 and 3). In the bee I note that there are three of these fibrillar masses, all easily recognized in frontal, but less so in horizontal sections (f. m. 1). The outer mass presents a lunar appearance in frontal sections, and lies close inside the basement membrane of the retina, being separated from it by sufficient space for the entrance of large tracheal sacs and a thin layer of cells commingled with the fibers from the retina.

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[1] The Brain of the Bee. Journ. Comp. Neurology. Vol. VI. Fasc. 3, 1896. pp. 133–210.

Earlier authors, from the time of the first good description of the finer structure of the optic lobes by Berger, to Carrière and Viallanes, evidently did not understand the significance of this outer fibrillar mass. Berger and Carrière considered it as forming a portion of the retina, and Viallanes found in it, in the case of the dragon-fly, structures that he denominated neuromatidia—structures unrecognizable in the bee, and really without existence in any of the arthropoda. The earlier description given by Hickson much more nearly approaches the truth, but this author erred in supposing what he saw to be protoplasmic reticuli. The first correct understanding of this body was arrived at by Parker, in his application of methylene -blue to *Astacus.* But between the crustacea, as noted by Parker, and the hexapoda, there are certain differences of detail that are readily apparent upon a comparison of the figure accompanying this paper and that given by the author mentioned.

Somewhat inside of this mass is the first or outer chiasma (x)—to be distinguished as such only in horizontal sections.

Concerning the two inner fibrillar masses it is to be noted that each is composed of two lenticular finally granular, or better, in the light of the new neurology, finely fibrillated masses separated by a loose mass of fibers that never assume so dark an appearance in the ordinary stains. Each body would, if it were a perfect segment of a sphere, form a meniscus lenticular mass whose convex surface is directed outward.

From the middle or second fibrillar body two tracts of fibers pass into the central cerebral mass as noted in my earlier paper. Each arises from the inter-lenticular mass of loose fibers and emerges at nearly the same spot with its fellow on the anterior side of the body. One passes inward and upward, becoming what I have called the *antero-superior optic tract,* which finally terminates among the dendritic fibrils of the cells of the adjacent mushroom bodies (*a-s o. t.*). The fibers of this tract originate, as has previously been pointed out, from a group of cells lying above the optic body (*op. b*) and below the anterior surface of the calyx of the outer mushroom body.

The cells and their processes passing inward towards the stalks of the mushroom bodies can be readily distinguished in preparations by von Rath's platino-aceto-picro-osmic acid, or by my formalin-copper-hæmatoxylin, method, and in one instance I was able to follow through consecutive sections, in a bichromate of silver preparation, the entire course of the fibers from the cells in their antero-superior position in the central cerebrum to their T-like branching before the outer stalk, and thence into the inter-lenticular portion of the second fibrillar body.

The other group of fibers, after passing inward and slightly downward for a short distance, turns and passes backward between the inner fibrillar body and the central cerebrum, entering the latter posteriorly at a level below the roots of the mushroom bodies. This I have described as the *antero-posterior optic tract* (*a. p. o. t.*).

Just where the cells of origin of this tract of fibers are situated has not yet been determined. It may, however, be mentioned, that I have found in preparations by the bichromate of silver method, cells, situated near the anterior edge of the second fibrillar mass sending, in several cases, their processes into the loose inter-lenticular mass. It may be that these are the cells of origin of the tract (4).

Tracts of fibers are likewise found issuing from the interlenticular space of the inner or third fibrillar body. They are not, however, restricted to one spot in finding egress, but issue along the entire hinder margin of the body; and it is rather difficult to distinguish them otherwise than as the *posterior optic tracts.* Their number varies according to the plane of sectioning, and, it may be, also with different individuals. There are chiefly to be noted, however, first, an upper tract that seems to pass over the median line of the brain to the inner body of the opposite lobe. This tract undoubtedly gives off branches by the way, and it is possible that the cells of origin of its fibers are to be found on the posterior side of the brain below the inner mushroom bodies. At a level somewhat below the inner roots of the mushroom bodies there is another tract that takes a nearly straight course from one inner body to the other on the opposite side of the brain. From this tract Viallanes was unable to find evidence of lateral fibrillar branches in the central cerebrum, and, after all the methods employed by me, I am compelled to say that I have been able to do little better. In one preparation by my formalin-hæmatoxylin method there seems to be evidence of such branches; but I have found no such evidence in bichromate of silver preparations. Finally, there are several small tracts below the last that terminate in the adjacent region of the central portion of the brain, and in the neighborhood of the terminations of the antero posterior optic tract.

The situation of the cells of origin of these tracts has not been definitely determined, but some of them no doubt may be found in the neighboring posterior mass of cells (5 and 6).

Two other tracts of fibres leave the inner fibrillar body. From the inner or concave surface of this there issue a large number of fibers that appear to be gathered up into two bundles. One of these passes forward as the *anterior optic tract* and terminates in the optic body (a, o, t; op. b), a small oval mass of fibrillar substance just above the antennal lobe. The other passes upward as the *postero-superior optic tract.* It joins the antero-superior tract for a short distance, and then passes behind the stalks and apparently into the calices of the mushroom bodies.

To this description and the one I gave in my former paper one might object, basing the objection upon the course and peculiarities of the fibers of the antero-superior tract, that since there is a tract of fibers connecting the inter-lenticular space of the second fibrillar body with the calices of the mushroom bodies, one would expect to find this posterior tract making similar connections with the inner body. The point was a difficult one to decide, and caused me an expenditure of considerable time in coming to a conclusion; but the evidence of my sections, both those by the formalin-copper-hæmatoxylin and those by the bichromate of silver, especially the latter, method, appears to be in favor of the description that I have given.

Considering now the denser mass of the fibrillar bodies it may be said that in sections treated by the formalin-copper-hæmatoxylin method one may find evidence of fibers passing through them in a direction nearly at right angles to their two surfaces. But such evidence is always fragmentary, and it is not until one employs the bichromate of silver method and thick sections that one is able to find unbroken individual fibres passing thus from one side to the other. Such fibers always show short arborescent branches in the outer and also in the inner lenticular mass. From the inner surface of the second fibrillar body they pass inward to the outer surface of the third body, which they enter, terminating arborescently a little below the surface. In this passage from one mass to the other they form, as seen in horizontal sections, a chiasma; so that a fiber emerging from the anterior side of the middle body enters on the posterior side of the inner body.

In many instances cellular connections were seen with the fragments of fibers crossing the masses and presenting the short lateral branches mentioned. In such instances the impregnated cells were found in the groups of cells lying anteriorly and posteriorly near the fibrillar bodies (2, 2′, 2″, 3, 3′, 3″). Their processes do not always enter the fibrillar bodies immediately upon reaching them, but run along the surface, curving around the fibers that do enter, and altogether presenting a somewhat lattice-like appearance when viewed at right angles to the surface of the body.

From the inner mass such crossing fibers have frequently been readily traceable into the anterior tract going to the optic body, but not into the postero-superior tract, which I was obliged to make out in heavily impregnated specimens.

From the outer surface of the middle body individual fibres have often been traceable nearly to the basement membrane of the retina, each posterior fiber crossing to the anterior side, forming with the anterior fibers the outer chiasma, and outside of this the peculiar palisade-like appearance that has been noted by the earlier authors.

Such fibers terminate proximally in the outer lenticular portion of the middle body in fine branchlets. Now and then a fiber entering this mass apparently from the palisade-like group of fibers gives off a few lateral branchlets and continues to the opposite side. Such cases I have interpreted to be the processes of the cells belonging to this middle body, but which have not been impregnated.

In other instances than those showing the fibers throughout their course nearly to the basement membrane of the retina, one finds fibers, or fiber groups, entering from each retinal element and continuing for some distance in through the palisade of fibers.

In some cases cells belonging to the group just inside of the basement membrane, which were described by Berger as the cells of the granular layer, are found impregnated and with their processes connecting with the fibres just described. In other instances fibers with short lateral branchlets are to be noted, the branchlets occurring in the region of the outer fibrillar body.

From the details noted it appears that the elements from the retina terminate each in a small tuft of fine branches in the outer fibrillar body, and come in contact with the fine lateral branchlets given off in the same region by fibers originating from the cells in Berger's granular layer. These latter fibers, forming elements No. 1, then continue on through the outer body, forming the palisade-like arrangement of fibers and the outer chiasma, and finally terminate arborescently in the outer lenticular mass of the middle body. The reasons that fibers from the retina seem to cross the outer body, forming a continuous passage between the basement membrane and the middle body is, it seems, that the lateral branchlets of elements No. 1 are very short, and the two small fibers are so closely applied together as to appear as one where they are heavily impregnated with bichromate of silver.

From the elements forming the optic lobes of the higher crustucea, as described by Parker, these and the elements belonging to the middle and the inner fibrillar bodies, noted in the figure as elements 2 and 3 respectively, differ in not forming a T-like figure, or in having a group of short lateral dendrites rather than one dendritic branch. This difference, it is plain, depends upon the location of the cell-body of the element. In the crustacea the latter, as shown by Parker, is situated between the fibrillar bodies that the two branches of its process connect. In the bee it is situated outside of the outer of the two bodies that are connected.

In summarizing the matter as just described, and as shown in my drawings and sections, it appears that, setting aside the outer or retinal elements, there are concerned in the transmission of visual stimuli to the central portion of the brain some six or seven neural elements, and that such stimuli may reach (1) the optic body, (2) the mushroom bodies, and (3) the hinder lower portion of the brain, and that they may pass over one or the other of the optic commissures—provided the upper one is a real commissure—to the inner fibrillar body of the opposite lobe, and thus indirectly reach the mushroom bodies, the optic body, and the posterior region of the brain on the opposite side. Further, it may be seen that there may be either three or four, or possibly more—but at least three—neural elements concerned in the transmission of a single stimulus. Thus, a stimulus may reach the optic body, the mushroom bodies, and the lower posterior portion of the brain as follows:

The mushroom bodies,	
By three elements,	1 a—2 b—(a.–s.ot.r.) or
	1 a—2 b—3 d.
The optic body,	
By three elements,	1 a—2 b—3 d.
The lower-hinder brain,	
By three elements,	1 a—2 b—(a.p.t).
By four elements,	1 a—2 b—3 d—(p.o.t.).

Further it appears that a single stimulus might reach all three cerebral centers.

This explanation seems to accord best with the existence of two sets of fibrillar branchlets upon one element (b.c. and d.e.); but it must be held to be hypothetical, since I have not been able to ascertain definitely whether the terminals of the fibers of the posterior, the antero-superior, and the antero-posterior optic tracts connect only with the secondary branchlets (c and e). If connections are made with the primary sets (b and d) then the matter becomes much more complicated.

EXPLANATION OF PLATE.

(DIAGRAMATIC.)

a, a′, a″.	Outer fibrillar connections in the outer fibrillar body.
a.o.t.	Anterior optic tract.[2]
a.–p.o.t.	Antero-posterior optic tract.
a.–s.o.t.	Antero-superior optic tract.
b, b′, b″.	Fibrillar connections in the outer lenticular mass of the middle body.
b.m.	Basement membrane of the retina.
c, c′, c″.	Fibrillar connections of the inner lenticular mass of the middle body.
d, d′, d″.	Fibrillar connections of the outer lenticular mass of the inner body.
D.c.	Dorso-cerebrum.
e, e′, e″.	Fibrillar connections of the inner lenticular mass of the inner body.
f.m. 1, 2, 3.	Fibrillar bodies 1, 2 and 3, or outer, middle, and inner.
l.o.c.	Lower optic commissure.
p.o.t.	Posterior optic tracts.
p.–s.o.t.	Postero-superior optic tract.
st.	Stalk of the outer mushroom body.
u.o.c.	Upper optic commissure.
4, 5, 6.	Supposed location of the cells of origin of the fibers of the *a.–p.o.t.* and the *p.o.t.*
x.	The outer chiasma.
z.	The inner chiasma.

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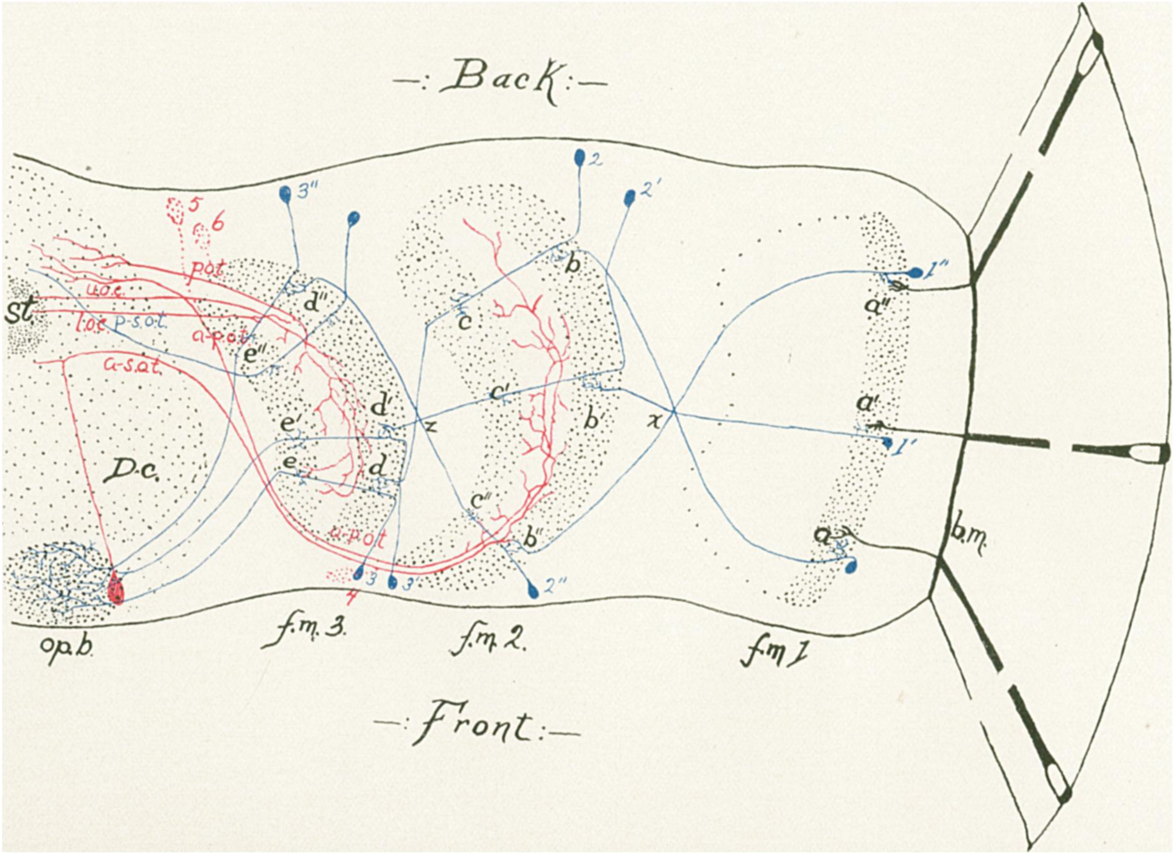
[2] The tract to the optic body (op. b.)

PLATE IX.



The Optic Lobe of the Bee's Brain.